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THE BIOLOGY OF *TORREORNIS INEXPECTATA* I. A COMPARISON OF VOCALIZATIONS IN *T. I. INEXPECTATA* AND *T. I. SIGMANI*

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The Zapata Finch (*Torreornis inexpectata*) is endemic to Cuba in three remarkably different habitats. The first population, consisting today of about 250 individuals, was discovered in the Zapata Swamp near the town of Santo Tomas, in 1926 (Barbour and Peters 1927). The second population (*T. i. sigmani*), separated by 720 km from the Zapata Swamp was not discovered until 1959 (Spence and Smith 1961) and inhabits the driest area in Cuba, a coastal zone dominated by the shrub called coastal incense (*Tournefortia gnaphalodes*) near the town of Baitiquiri on the southeastern tip of Cuba (Fig. 1). This population consists of 55-100 pairs. A third population (*T. i. varonai*), discovered in semideciduous dry forest and thorn scrub on Cayo Coco on the northern coast in the mid-1970's, has recently been described (Regalado 1981).

Little was known about the biology of the first two populations until two expeditions, of which the authors were members, by the Instituto de Zoología of the Cuban Academy of Sciences studied various aspects of the ecology and behavior of the species. This report emphasizes the acoustic communication of *Torreornis*; future publications will cover the species' ecology, demography, conservation, and natural history.

Torreornis is thought to be related to the emberizine genus *Aimophila* (Paynter and Storer 1970). The rufescent crown and black malar stripe do resemble these features in some members of that genus (see frontispiece). The subspecies of *Torreornis* are similar in size, but the eastern population is much duller, with the rufous on the crown and the yellow of the breast less intense, than those finches found in the humid Zapata Swamp. The emberizine finches are well known for inter-population song differences. Through song learning, local song dialects may develop (Marler and Ta-

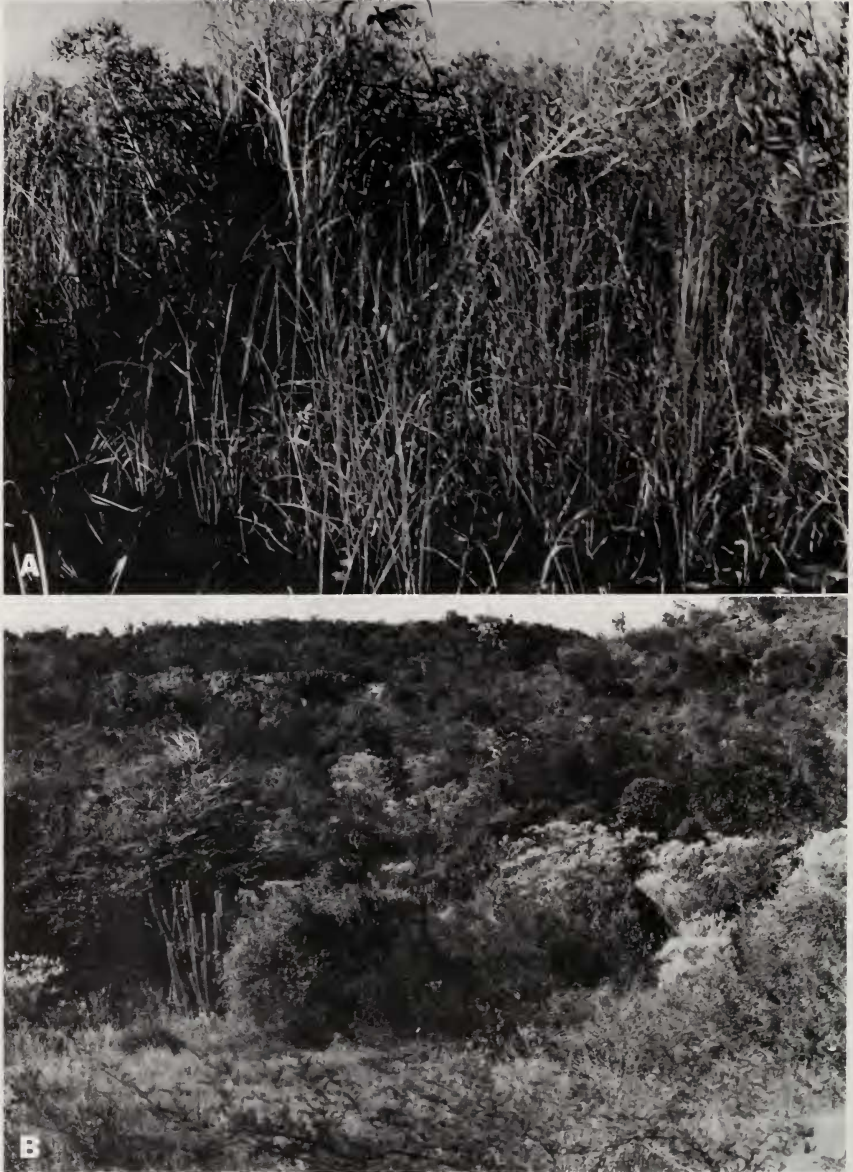


FIG. 1. Habitats of *T. inexpectata*. (A) *Myrica* and sawgrass hummock surrounded by water used by *T. i. inexpectata* in the Zapata Swamp. (B) Dense cactus and thorn scrub habitat of *T. i. sigmani* 5 km W of Tortuguilla. *Torreornis* habitat is indicated by the light colored leaves of coastal incense (*Tournefortia gnaphalodes*), right center; *Torreornis* eats its small seed pods.

mura 1964), especially if the populations are non-migratory (Baptista 1976). Differences in the acoustics of habitats may also select for differences in the types of sounds used in long distance communication. For example, forest birds tend to use clear tones, whereas birds of grassland and marshes use highly frequency-modulated sounds (Morton 1975). Thus, one might expect that populations of *Torreornis* living in a near-desert community (*T. i. sigmani*) would be under a different acoustical regime than *T. i. inexpectata* in its sawgrass, *Myrica* hummock-filled swamp habitat. The 720 km now separating these populations would insure that no recent contact might affect a resemblance in their vocalizations through cultural exchange. The purposes of this report, therefore, are to describe the vocal behavior of *Torreornis* and to compare and contrast the vocal behavior in the two populations.

METHODS

Recordings were made with a Uher 4000 Report tape recorder at a tape speed of 19 cm/sec with a Dan Gibson 46.2 cm diameter parabolic reflector. Sounds were analyzed on a Kay Elemetrics Company Sonagraph model 7029 using the wide band filter and with a Princeton Applied Research Real Time Spectrum Analyzer model 4512 coupled to a Unigon Scan Converter. All illustrations were made from sonagram traces.

Recordings were obtained of *T. i. inexpectata* during the "Expedition Florentino Garcia Montaña" to the Zapata Swamp from 25 October–1 November 1979; those of *T. i. sigmani* were made from 2–5 November 1980. Tape recordings of song and callnotes were used to elicit responses from pairs; playbacks of songs of *T. i. inexpectata* to individuals of *T. i. sigmani* resulted in prompt responses and song displays. Playbacks were used to lure pairs into mist nets for capture and color banding.

RESULTS

General behavior.—*Torreornis* exists in pairs that appear to defend territories throughout the year. Neither population was breeding during our study of vocal behavior, yet pairs responded to playback of the duet song by flying toward the sound, then perching conspicuously. Duets occurred when one bird, usually the male, flew to a new perch followed by the female. Immediately upon landing, the birds perched within 7–30 cm of one another and, with wings waving slowly, sang one of their forms of duet song (see below). When pair members were separated, the buzz call-note was given by either sex as a contact note. Often the first response to a song playback would be rapid chip notes as one bird flew toward the source of the sound. One bird from each population was recorded as it gave distress sounds upon being removed from a mist net. These then were the four general classes of vocalizations recorded from both populations of *Torreornis*: song (includes duet and single bird songs), chips, buzz calls, and distress call. *Torreornis* thus has a simple vocal repertoire although structural variation occurs within each of the four general classes

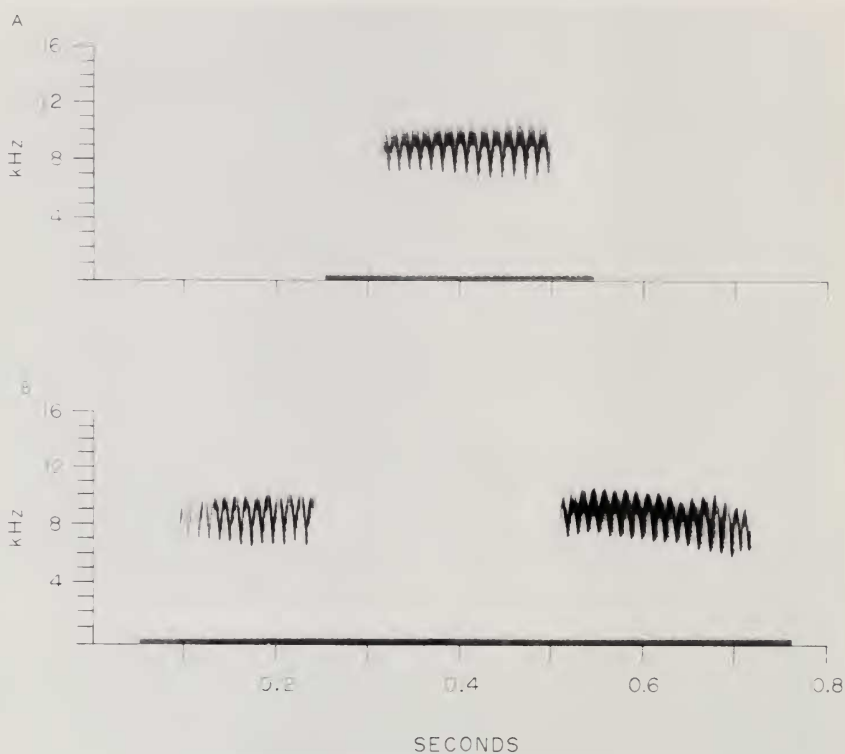


FIG. 2. Buzz callnotes of *T. i. inexpectata* (see text). This and all other figures are from wide band spectrograms.

of sounds. The duet was remarkably complex with respect to the timing of each pair-member's contribution to it and to changes in note structure during a single duet.

During the expedition to study *T. i. sigmani*, important differences between the sexes were noted that allowed us to sex birds in the field, even though the species is monomorphic. Males would nearly always precede females while the pair was responding to a song playback in their territory. Second, males often gave two to four contact buzz notes in a series, whereas females only gave single buzz notes. We do not know if the same holds true for *T. i. inexpectata*. The sexual difference for *T. i. sigmani* was confirmed for us after several birds were collected for specimens.

We now describe in more detail the variation in sound structure within each of the four vocalization classes.

The buzz call.—Buzz calls are illustrated in Fig. 2 for *T. i. inexpectata*

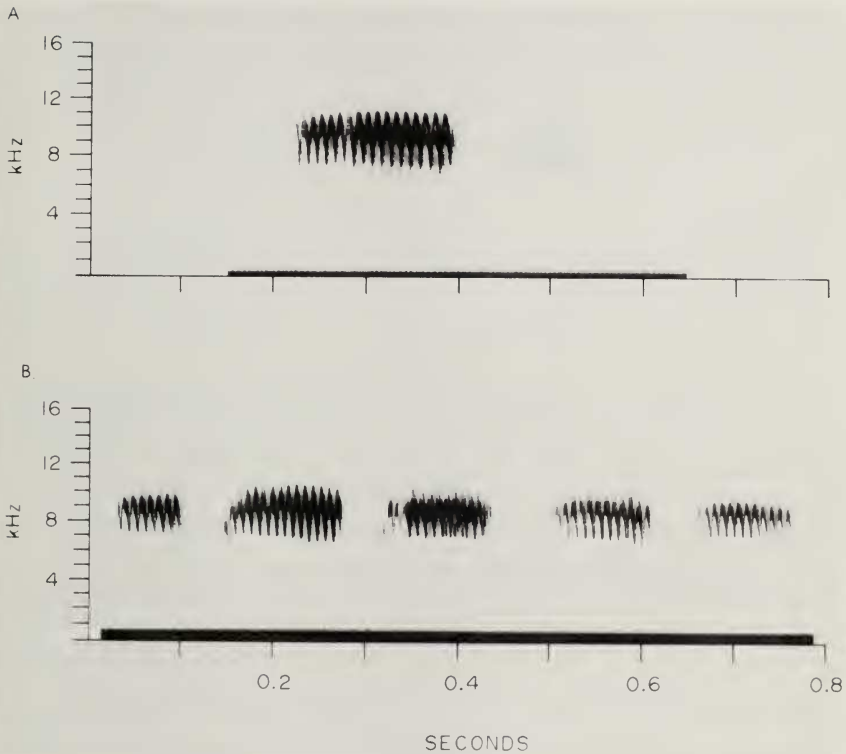


FIG. 3. Buzz callnotes of *T. i. sigmani* (see text).

and in Fig. 3 for *T. i. sigmani*. This is the most commonly heard sound and is the sound that betrays the presence of this difficult-to-see finch to the human observer. To the human ear it sounds like a high pitched *zee* or *zeea* of varying duration, but the spectrograms prove that it has a complex sound structure.

T. i. inexpectata buzz calls modulate in frequency between 5.3–10.9 kHz with a carrier frequency from 8–10 kHz. *T. i. sigmani* buzz calls range from 7.5–13 kHz with a carrier frequency at 9–10 kHz. There is also a difference in the modulation rate: *T. i. inexpectata* calls are modulated in frequency at a rate ranging from 90–100 Hz, whereas *T. i. sigmani* buzz calls are frequency modulated at a rate of from 110–120 Hz ($t = 12.1711$, $P < 0.001$). This difference is easily seen if Figs. 2 and 3 are compared: *T. i. sigmani* calls appear like a compressed spring while *T. i. inexpectata* calls look like a less compressed spring, reflecting the difference in modulating rates.

Although the modulation rate does not change during a buzz call, the frequency range of the modulation does change in some calls. In Figs. 2A and 3A, the frequency range of the modulation increases 1 kHz part way through the call. This is indicated by the sudden increase in the width of the spectrogram trace. The increase in frequency range is due to the inclusion of lower frequencies, not higher frequencies into the sweep of the modulation.

Buzz calls also vary in their rate of repetition (contrast Fig. 2B with Fig. 3B) and they may decrease in overall frequency (Fig. 2B at right) or they may rise and fall in frequency. All of these variations are easily apparent to the human listener. Individual buzz calls also ranged from 0.07–0.25 sec in duration.

These variations are associated with the nearness of the mate and whether or not the mate is also giving callnotes. A lone bird utters isolated buzz calls of long duration. If the mate appears to respond, the buzz calls tend to rise or to rise and fall in carrier frequency. Males in the *T. i. sigmani* population seemed to use series of three to five buzz calls more often than males of *T. i. inexpectata* (Fig. 3B).

Buzz calls were uttered while mates were foraging on the ground out of visual contact with one another and also during reactions to playbacks of tape recorded songs. The buzz calls appear to function to keep mates in contact and probably also function to keep family groups in contact. We never observed more than two birds together in the *T. i. sigmani* population, but *T. i. inexpectata* occurred in groups of three or four as well as in pairs at the same time of year. Perhaps the breeding season is later in the Zapata Swamp and family groups have not yet broken up. Ripley and Watson (1956) also found *T. i. inexpectata* in small groups in October. Since *Torreornis* reacts aggressively to played-back song, defending year-long territories (Gonzalez, pers. obs. of color banded birds), these groups are likely to consist of family groups rather than indicating a general social flocking tendency. It remains to be determined if *T. i. inexpectata* males have sex-characteristic series of buzz calls as do *T. i. sigmani* males.

Distress call.—Distress calls (Fig. 4A, *T. i. inexpectata*; Fig. 5A, *T. i. sigmani*) were recorded from one captured bird from each population. One free *T. i. sigmani* female gave distress calls identical in physical structure to those of the bird in Fig. 5A, when briefly attacked by her mate. Distress calls have a regular modulation in frequency at a rate of 60 cps in the *T. i. inexpectata* example, through a frequency range of about 4–9 kHz. They are short in duration (ca. 0.1 sec) and are delivered at variable rates. *T. i. sigmani* distress calls are not frequency modulated in a regular fashion. Distress calls in both populations differ from buzz calls in being lower in frequency and in having more abrupt changes in frequency at the maximum and minimum.

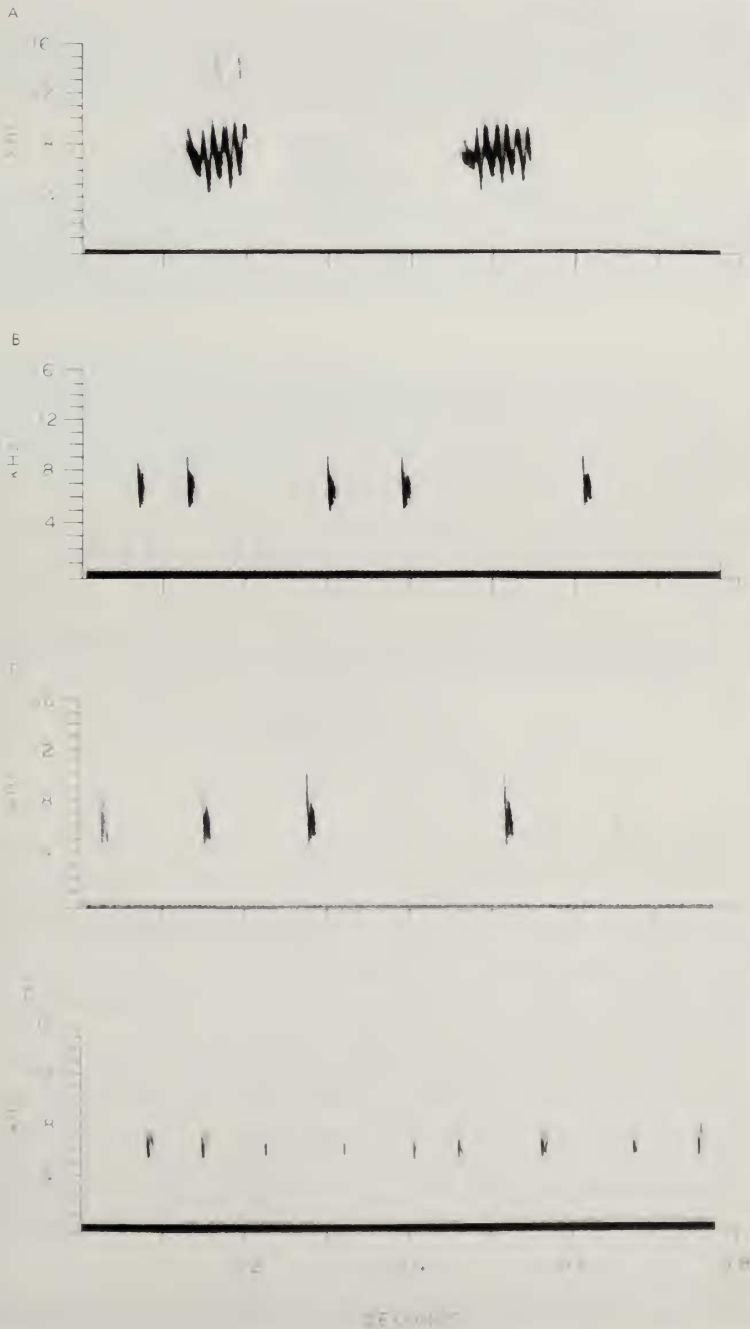


FIG. 4. A. Distress calls. B-D. Chips (*T. i. inexpectata*).

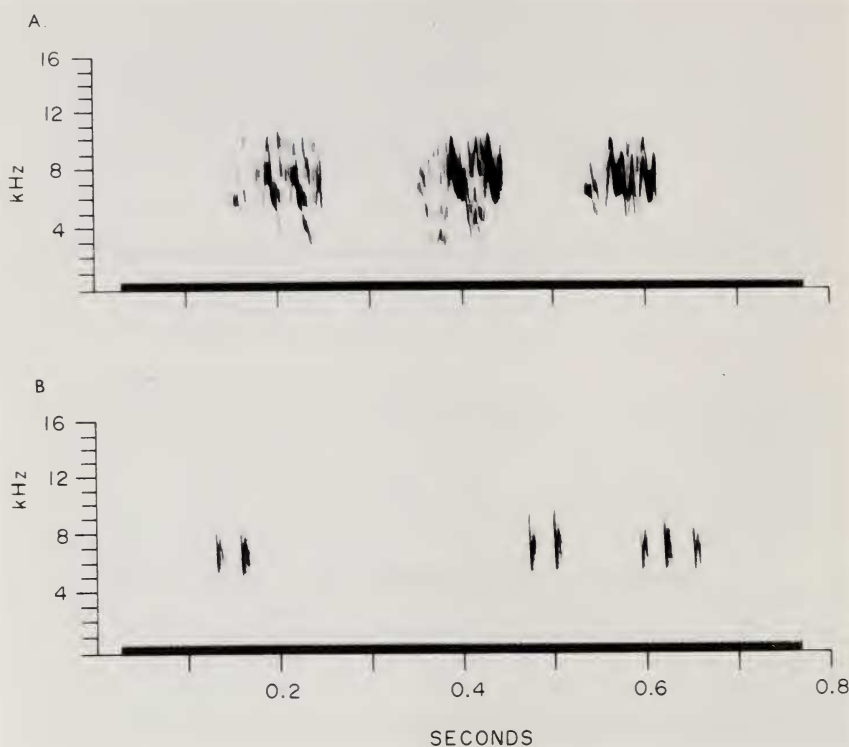


FIG. 5. A. Distress calls. B. Chips (*T. i. sigmani*).

Distress calls occur when a bird is unable to escape from a frightening stimulus as when captured by humans or attacked inadvertently by a mate looking for a territorial intruder. Whether the obvious differences in distress call structure in Fig. 4A and 5A reflect true differences between the populations is uncertain and must await a larger sample.

Chips.—Chips were identical in the two populations (Fig. 4B–D, *T. i. inexpectata*; Fig. 5B, *T. i. sigmani*). They varied greatly in rate, from single notes to rapid rates up to 20 per sec. Each chip consists of an initial rapid, pulse-like down-swept frequency modulation followed by a chevron-shaped up-then-down frequency change, within about 0.01 sec. The frequency ranges of chips also varied. Chips were sometimes delivered rapidly in bouts of two or three as in Fig. 4B.

The rate of chip delivery appeared to vary directly with how aroused or stimulated the calling bird was. A bird responding to a played back re-

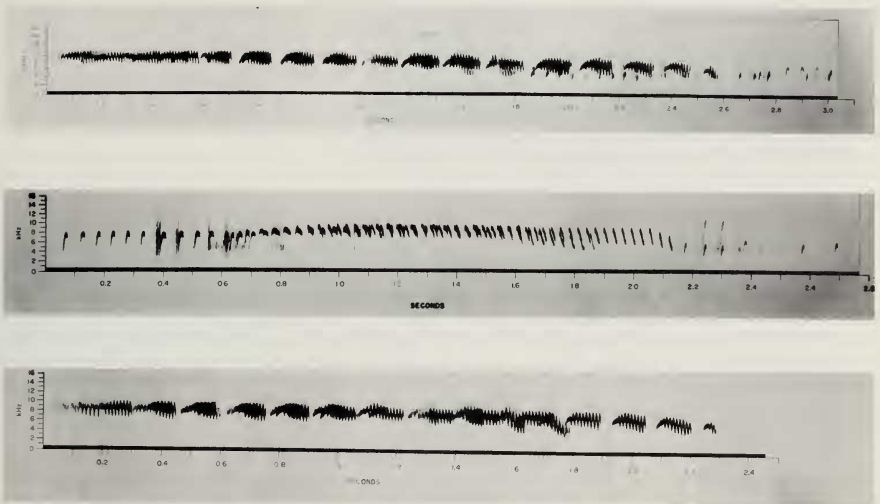


FIG. 6. Duet songs of *T. i. inexpectata*. Buzz duets (top and bottom); chatter duet (middle).

coding of song uttered its most rapid chips as it flew toward the tape recorder for the first time. The rate would decrease thereafter. Chips appear to be similar in function and used in similar contexts to similar callnotes found in many species of small passerine birds. Some stimulus, usually a predator or an intruding conspecific, is perceived that arouses the calling bird.

Song.—*Torreornis* pairs sing spectacularly intricate duets which are, to our knowledge, the only New World example of duets containing completely synchronized syllables. Duet syllables are either frequency modulated (buzz duets) (Fig. 6, bottom), pulse-like upslurs and/or downslurs (chatter duets) (Fig. 6, middle; Fig. 7, top). Duets may consist entirely of one or the other or contain both syllable types (Fig. 6, top, bottom). No difference in duet duration or syllable number per duet was found when comparing the two populations (Table 1).

All duets characteristically increase in amplitude, reaching a peak which is held for most of the duration, with a decrease toward the end. Often one or both birds change to chatter syllables at the end of a duet. The middle portion is 13.5 db greater in amplitude than the beginning or end, probably due to the complete synchronization that occurs in this portion. If these synchronous sounds are in phase the resulting amplification should permit the song to be broadcast over a larger area than if the synchronization was less precise. This cooperation in singing has not been previously

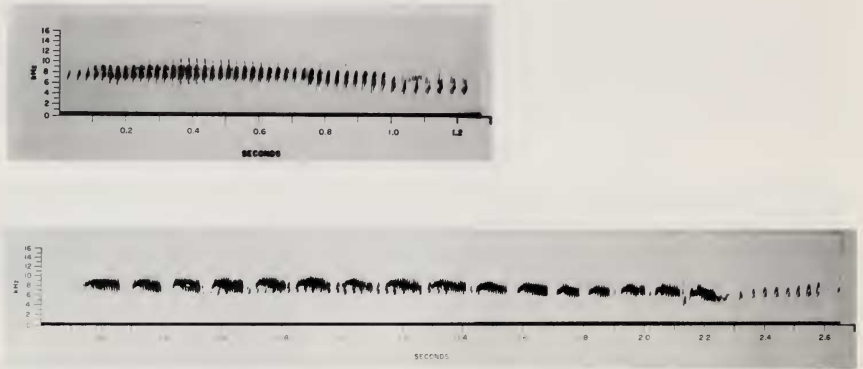


FIG. 7. Duet songs of *T. i. sigmani*. Combination buzz and chatter duet (bottom); chatter duet (top).

reported and may signify strong selection for mate cooperation in territorial defense.

We believe the male usually begins the song and his mate quickly joins in. Fig. 6 (top and bottom) illustrates the development of synchrony from the song beginning to about 0.6 sec. From then on, the rapid frequency modulated buzzes stay in perfect synchrony until one bird decreases its buzz frequency at 1.6 sec before changing from buzz to chatter syllables (Fig. 6, top) from 1.85 sec to the end of the song. Another duet from *T. i. inexpectata* (Fig. 6, bottom) included a frequency drop by one bird at 1.6 sec into the song. In this duet they lost the synchrony in buzz syllables, and neither pair member switched to chatter syllables. The chatter duet also exhibits syllable synchrony. In Fig. 7 (top), one bird begins with three notes, whereupon the second begins singing slightly higher frequency notes of the same shape as the initiator's; each lowers its note's frequency in synchrony after 0.75 sec into the song.

Each pair of *Torreornis* varies the structure of successive renditions of its song duets to such an extent that we could not distinguish pair-distinctive patterns. It was our impression that pairs of *T. i. inexpectata* sang proportionally more buzz duets, but the sample consisted of only four pairs. Both members used buzz syllables in two of 17 duets from *T. i. sigmani* (this sample of 10 pairs was ca 20% of the total population). In 11 of the 17, the male used buzz syllables while the female used chatter syllables as shown in Fig. 7 (bottom). However, we believe that chatter songs are more likely to occur as the first few songs sung in response to playback. For the *T. i. sigmani* study, we used a tape loop of *T. i. inexpectata* buzz duet for the stimulus and repeated it more frequently. For *T. i. inexpectata*, we used primarily playbacks of the buzz callnote to

TABLE I
COMPOSITION OF DUET SONGS COMPARING *T. I. INEXPECTATA* AND *T. I. SIGMANI*

Number of syllables ^a	Syllable type		Overall song length (sec)	Frequency range (kHz)
	buzz	chatter		
<i>T. i. inexpectata</i>				
25	8	17	3.5	7-11
47	0	47	3.2	4-8
89	0	80	4.2	4-10
34	19	15	5.0	5-11
33	19	14	4.3	4-10
47	14	33	5.2	4-10
37	17	20	5.2	3-11
25	19	6	4.4	6.5-11
52	14	38	5.1	4-11
36	17	19	5.2	4-10
20	7	13	1.6	4-10
37	12	25	3.1	4-11
21	13	8	3.4	4-11
N = 13				
$\bar{x} = 38.7 \pm 18.14$			$\bar{x} = 4.1 \pm 1.10$	
<i>T. i. sigmani</i>				
15	15	0	3.2	6-10
15	15	0	3.4	6.5-9.5
52	7	45	3.1	4-9.5
46	0	46	1.9	4-9.5
64	1	63	2.5	4-9.5
53	0	53	2.1	4-9
26	11	15	2.9	4-10
16	11	5	2.6	5-10
64	6	59	2.6	4-10
85	3	82	3.4	4-9
9	9	0	2.6	6-11
51	0	51	2.2	5-10
58	17	41	3.8	5-10
61	1	60	2.5	4-9
47	2	45	1.8	6-9
N = 15				
$\bar{x} = 44.1 \pm 22.66$			$\bar{x} = 2.7 \pm 0.58$	

^a Neither population differed significantly in number of syllables or overall song length (*t*-test).

stimulate pairs, because we had nothing else. It is likely that the chatter duet is delivered by highly aroused birds, because these occurred immediately following playback in both populations and often followed aggression by one pair member toward the other just before they duetted.

We heard few natural duet songs. Even after a playback, duets were delivered only after a flight towards the source of the playback. The birds mostly looked for the "intruders" while perched high in vegetation.

DISCUSSION

T. inexpectata exhibits little difference in its four classes of sounds in two isolated populations. Distinct song differences have not developed despite the distance and long time period that separates the two populations. The only major difference appears in the modulation rate of the buzz callnote, *T. i. sigmani* having a faster rate than *T. i. inexpectata*. Buzz songs are more alike in the populations than chatter songs. *T. i. inexpectata* have chatter songs composed of three different elements that change from upslurred to downslurred during a song, whereas *T. i. sigmani* songs consist of upslurred elements. The extant populations are undoubtedly remnants, for fossils are known from caves outside the present range of the species (Pregill and Olson 1981). The current habitat differences (swamp vs arid scrub) may not differ in acoustic properties since the Zapata Swamp is nearly dry at certain times of the year, resulting in a habitat more like that of scrub grassland (Olson, pers. comm.).

Regalado (1981) describes three of the vocalizations of *T. i. varonai* from Cayo Coco as *tsik*, *chrii*, and song, which are similar to and correspond with our chip, buzz, and song. However, he mistakenly describes the song as a territorial duel between two males rather than a duet between a pair.

Like many other tropical passerines which have permanent territories and permanent pairbonds, duets appear to function in territorial defense (Farabaugh, in press). In addition, duets may evolve specifically to increase the effectiveness of territorial defense through reducing potential misguided aggression toward the pair member in the context of territorial intrusion. By coming in close proximity to one another, the pair members of monomorphic species, such as *Torreornis*, may avoid mistaking each other for an intruder and therefore more efficiently direct their aggression toward the real intruder. Synchrony may increase the duet's amplitude such that potential intruders are repelled at greater distances.

Given the emberizine heritage of *Torreornis*, it is remarkable that a greater difference in song was not found between the populations. Perhaps the fact that both sexes contribute to the complicated, synchronized duet, places constraints on divergence of the structure of the song. Perhaps individuals tending to diverge from the established song types are less apt to attract and maintain mates if potential mates are not able to effectively synchronize their songs with them.

The duet songs of *Torreornis* are similar in context of delivery to duet or chatter songs described for *Aimophila* sparrows (Wolf 1977) and to-

whees (*Pipilo* sp.) (Marshall 1964), but these also have male-only ("primary") songs which are lacking in *Torreornis*. The Rufous-crowned Sparrow (*Aimophila ruficeps*) chatter duet is structurally similar to a buzz-and-chatter-combination duet of *Torreornis* (see Wolf 1977:112). If *Torreornis* is closely related to *Aimophila*, as suggested by extensive morphological data (McKittrick, pers. comm.), then the loss of male-only song in *Torreornis* may have been coupled with a more complex development of the chatter or "pair reunion" duet found so extensively in *Aimophila*.

SUMMARY

The Zapata Finch (*Torreornis inexpectata*), endemic to Cuba, exists in three widely separated populations. Here we describe and compare the vocalizations of the Zapata Swamp population with the population living in a near-desert habitat 720 km to the east, near Baitiquiri. Adult *Torreornis* have a simple vocal repertoire of four sound types: chip, buzz, distress call, and song. Highly synchronous duet songs are used by pairs to defend territories throughout the year. The divergence in habitat and separation by distance have not resulted in major differences in the vocalizations of the two populations.

ACKNOWLEDGMENTS

The two expeditions permitting this study were superbly planned and logistically supported by the Instituto de Zoología of the Cuban Academy of Sciences. Special gratitude is due to Dr. Fernando Gonzalez, Director of the Instituto de Zoología, for his support and assistance during all phases of this research. Noel Gonzalez provided much help and field companionship during the expedition to study *T. i. sigmani*. In addition, Dr. Storrs Olson of the Smithsonian Institution happily verified the sexes of *T. i. sigmani* specimens and was an enthusiastic member of both expeditions. Dr. James F. Lynch, also of the Smithsonian, provided insight to the study of *T. i. sigmani*. We thank Storrs Olson and Luis Baptista for reviewing the manuscript. Sigrid Bruch and Judy Gradwohl graciously prepared the illustrations. Travel funds were provided by Fluid Research Funds from the Smithsonian Institution and from Friends of the National Zoo.

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COLOR PLATE

The color plate Frontispiece of the Zapata Finch (*Torreornis inexpectata*) has been made possible by an endowment by George Miksch Sutton. Painting by John P. O'Neill.

FIRST ANNOUNCEMENT

XIX CONGRESSUS INTERNATIONALIS ORNITHOLOGICUS

At the XVIII International Ornithological Congress in Moscow the International Ornithological Committee accepted the invitation of the National Museum of Natural Sciences of Canada and of the Canadian ornithological community to hold the XIX Congress in Canada. The Congress will be held in Ottawa, Canada, from 22-29 June 1986. Dr. Prof. Klaus Immelmann (West Germany) was elected President of the Congress. Dr. Henri Ouellet (Canada) was designated as Secretary-General.

Details about the general and scientific programs, field excursions, and other activities during the Congress will be available later.

Those interested in participating in the Congress are urged to inform the Secretariat in order to obtain announcements and application forms. Correspondence should be addressed to The Secretary-General, Dr. Henri Ouellet, XIX Congressus Internationalis Ornithologicus, National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario K1A 0M8, Canada.